THE EFFECT OF THE CIRCULATION OF WATER ON THE DISTRIBUTION OF THE CALANOID COMMUNITY IN THE GULF OF MAINE [1]

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Damas (1905) has pointed out that the flow of water tends to dissipate local populations of pelagic organisms, and that the permanence of breeding stocks may be maintained by the existence of eddies. His predictions have been strikingly confirmed by hydrographic observations in the Norwegian Sea (Sømme, 1933). Along the margins of the Gulf of Maine the permanence of the stock of *Sagitta elegans* is correlated with the stability of the hydrographic conditions which exist in different regions (Redfield and Beale, 1940). Walford (1938) has indicated the importance of fluctuations in the circulation on Georges Bank to the fate of haddock eggs spawned in that region. These studies and that of the author (1939) on the population of *Limacina retroversa* emphasize the rapidity with which currents move pelagic organisms about within the Gulf. It becomes a problem whether the community of the basin of the Gulf is truly endemic, and by what mechanism a breeding stock is maintained within the Gulf. Sømme (1934) has discussed this question in regard to the copepod population of the Lofoten area.

Bigelow (1926), who has described the zoöplankton of the Gulf in great detail, considers that the species which form the bulk of the pelagic population are endemic in origin, breeding with sufficient regularity and abundance to maintain the local stock by local reproduction. From its dominating member, *Calanus finmarchicus,* he has referred to the population as the calanoid community.

We have measured the catches taken in the Gulf during a year-round survey and will attempt to explain the distribution of numerical abundance in terms of the pattern of currents obtained during the period of observation.

Data

The data employed in the present study were collected in the course of cruises made by the research vessel "Atlantis" during the years of 1933 and 1934. The dates of these cruises and the numbers of the

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stations occupied are given in Table I. Thirteen cruises were made in the course of fifteen months, with the result that 684 hydrographic stations in the Gulf of Maine and its adjacent waters were occupied. At no time did a period longer than two months elapse without observation. The routine hydrographic and chemical data are published in the Bulletin Hydrographique (1933, 1934).

A supplementary cruise was made in May, 1936 in order to confirm certain observations made during the primary survey.

In the course of the cruises standard vertical hauls were made with a 1.5 meter Heligoland net of No. 0 silk having 38 meshes to the inch (Künne, 1933). The net was hauled from a point near the bottom to the surface at all stations occupied, weather permitting. This type of haul was selected in preference to the oblique haul in the belief that the procedure could be carried out uniformly as a part of the routine duties

TABLE I

Cruise No.	Dates	Stations	Number
16 and 17	June 19–July 10, 1933	1643–1721	79
21	Sept. 2–Sept. 14, 1933	1741–1802	62
22	Oct. 17–Oct. 29, 1933	1803–1860	58
23	Dec. 2–Dec. 11, 1933	1861–1906	46
24	Jan. 8–Jan. 13, 1934	1907–1934	28
26	Mar. 21–Mar. 29, 1934	2019–2070	52
27 and 28	Apr. 17–May 13, 1934	2071–2164	94
29	May 21–June 3, 1934	2165–2215	51
31	June 25–July 1, 1934	2217–2236	20
34	Aug. 10–Aug. 11, 1934	2252–2259	8
37	Sept. 17–Sept. 27, 1934	2268–2303	36
55	May 14–May 19, 1936	2555–2583	29

of the ship's company. Unfortunately, it proved impossible to use the net in rough weather, so that data are lacking from many stations, particularly those made in the winter months. The yields of the successful hauls have been measured by collecting the plankton on filter paper in a Buchner funnel. Suction was continued until the preserving fluid ceased to flow, whereupon the "dry" plankton was introduced into a measured volume of fluid and the resulting increase in volume noted. The data so obtained were reduced to figures expressing the number of cubic centimeters of "dry" plankton under each square meter of the sea surface. Before filtering and measuring collections, any large gelatinous organisms were removed (*Salpa*, ctenophores, medusae) with the result that the measurements reflect primarily the abundance of the crustacean community.

Since most of the hauls with which we are concerned were made in

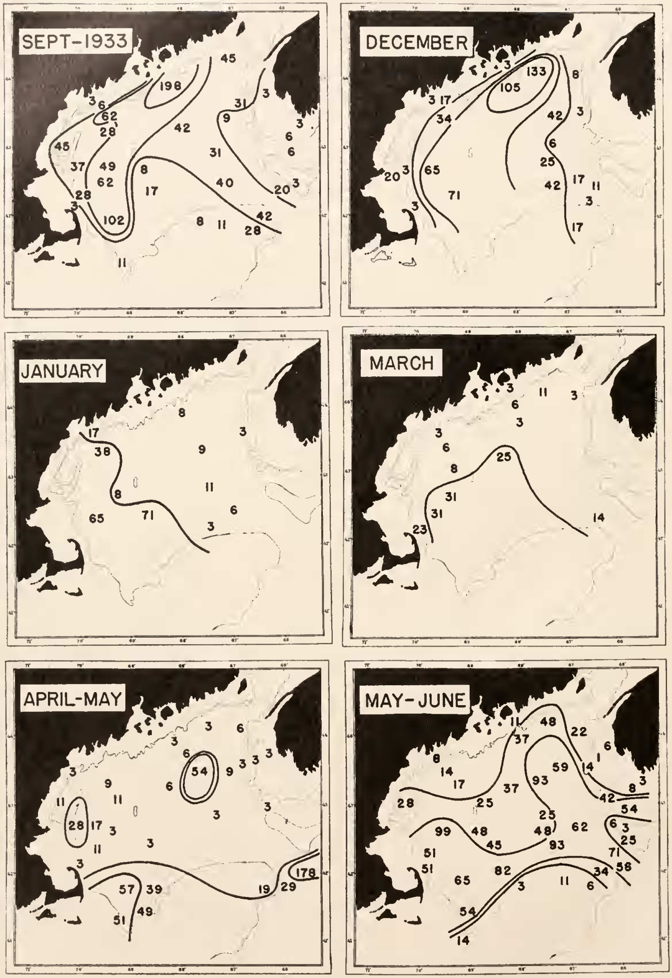

FIG. 1. Volumes of zoöplankton taken in vertical hauls between September, 1933 and June, 1934. Numbers represent the cubic centimeters taken per square meter of sea surface. Contour interval 25, 50, 100, and 200 cc. per square meter.

depths greater than 100 meters, above which level most of the population may be expected to occur, these figures are thought to express the density of population more precisely than numbers reduced to unit volume of water strained. The general character of the results is not altered by expressing the catch in terms of the yield per cubic meter.

The determination of the " dry " volume of the catch by the method of filtration and displacement yields smaller values than are obtained by the " wet " method of allowing the animals to settle in a calibrated container. In order that our results may be compared with those of Bigelow and others who employed the settling method, a number of samples have been measured by both methods. The wet method gave values on the average 4.9 times higher than the dry method, the ratios

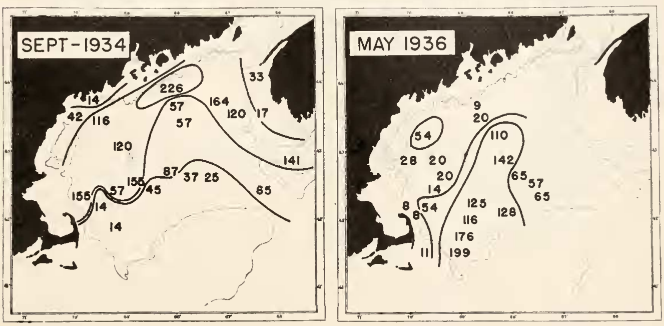

FIG. 2. Volumes of zoöplankton taken in vertical hauls in September, 1934 and May, 1936. Numbers represent the cubic centimeters taken per square meter of sea surface. Contour interval 50, 100, 200 cc. per square meter.

varying between 3.3 and 7. The ratio was smaller in the case of the larger samples, due perhaps to the tighter packing of large samples in the wet method and to the greater retention of water when large quantities of organisms are filtered off in the " dry " method.

The Seasonal Distribution of the Zoöplankton Population

The quantities of the catches obtained by vertical hauls, and their positions during the most complete periods of survey, are entered on the charts shown in Figs. 1 and 2. These charts show that the area of maximum abundance shifts its position with the season. From late summer until December the richest population is found in the northern portion of the Gulf, centering off Mount Desert. During the winter the center shifts to the west, coming to lie off the Massachusetts coast.

In late spring and early summer the richest catches were obtained along the southern margin of the Gulf, north of Georges Bank, extending from the offing of Cape Cod, eastward and northward toward the Bay of Fundy.

FIG. 3. Chart of the Gulf of Maine showing principal place names and the sectors into which the area is divided for analysis of population distribution. Contour encloses depths less than 100 meters.

In order to deal with the data statistically, the area of the Gulf has been divided into seven sectors as shown in Fig. 3. Each sector includes one of the principal lines of stations at which collections were regularly made. The quantities of plankton taken at each cruise in each sector have been averaged and the resulting number taken to represent the density of population in that sector at the time. While the data are frequently numerically inadequate, certain interesting regularities appear from its analysis.

Figure 4 shows the density of population in the various sectors at each principal period of survey. It presents graphically the shift in the center of population westward from the Mount Desert to the Massa-

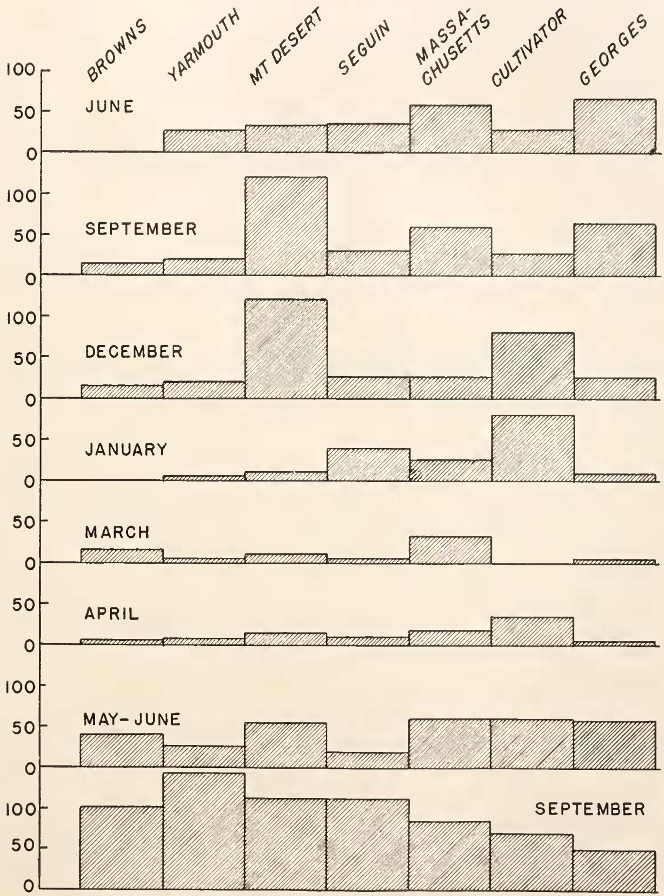

FIG. 4. The average catch in each sector of the Gulf of Maine during the period September, 1933 to September, 1934. Ordinates: cubic centimeters of zoöplankton per square meter of sea surface.

chusetts sector in the course of the winter and its extension along the southern sectors in May and June, followed by the reëstablishment of a maximal population in the northeastern sectors in September.

Figure 5 presents the same data in a form which brings out the sea-

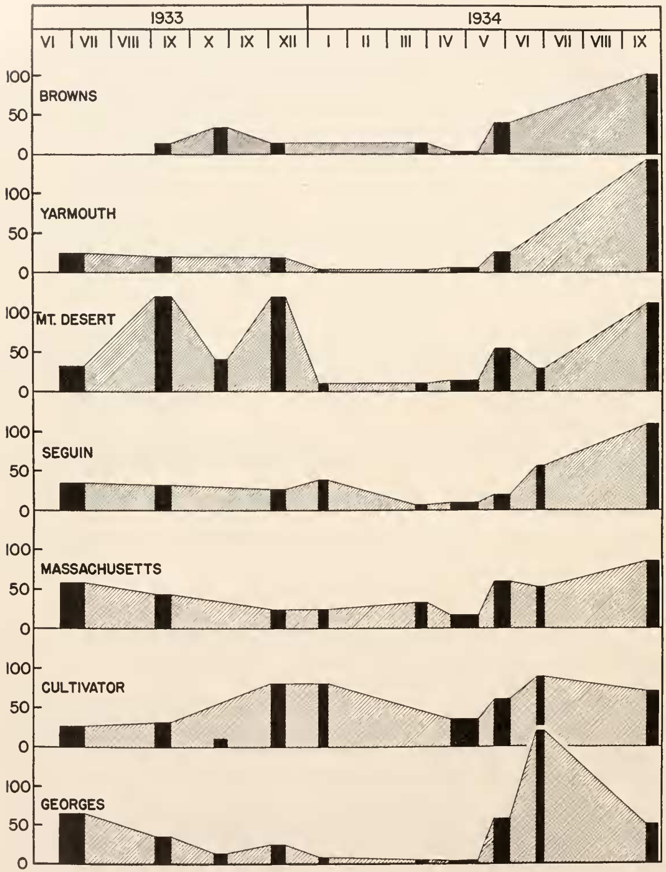

FIG. 5. Seasonal fluctuation of catch in each sector of the Gulf of Maine during the period June, 1933 to September, 1934. Ordinates: cubic centimeters of zoöplankton per square meter of sea surface. The black bars indicate the actual period occupied by each cruise.

sonal fluctuation in each sector. The sectors along the east and north sides of the Gulf are marked by a pronounced seasonal fluctuation—most extreme in the Mount Desert region. In contrast, the population is much more uniformly distributed from month to month in the Massachusetts and Cultivator sectors, which include the greater part of the western basin.

The general features of the distribution appear to recur from year to year, for our observations for September 1933 and 1934 show essentially similar patterns, as do also those for May–June, 1934 when compared with May, 1936. The seasonal distribution observed by Bigelow over a number of years is also in agreement. He found the quantitative fluctuations to be comparatively narrow from season to season in the waters of the western basin and considered the plankton in that part of the Gulf to be " rich " the year round. He reports the northern corner of the eastern basin, as well as the shallows off Cape Sable, to be the site of a wide seasonal fluctuation (Bigelow, 1926, p. 89).

The Circulation of the Gulf

The shift in the center of abundance of the zoöplankton population suggests that it is being borne about a great cyclonic eddy. We may consequently examine the nature of the circulation of the Gulf to see if it can account for the fluctuations in numbers in different places and to learn to what extent the calanoid community may be carried into and out of the Gulf by water movements.

The evidence marshalled by Bigelow (1927)—measurements with current meters, drift-bottles, temperatures, salinities, distribution of plankton, and dynamic calculations—can be harmonized with one type of dominant circulation only, a general anti-clockwise eddy around the basin of the Gulf. The demonstration of this, named by Huntsman (1924) and by Bigelow the " Maine " or " Gulf of Maine " eddy, with all it implies in its biological bearing, is perhaps the most interesting result of their joint explorations of the Gulf. Observations made during a series of years demonstrated that the center of the eddy shifted its precise location from summer to summer, and that marked seasonal variations in the circulatory scheme occurred. Observations of the velocity of the non-tidal drift of the surface made in shoal water about the margin of the Gulf indicated an average movement of seven miles per day, at which rate some three months would be required to complete the circuit of the eddy. No estimations were made of the velocity of the deeper layers.

The hydrographic data collected in the course of the cruises in 1933–34 have been analyzed by Dr. E. E. Watson, who has kindly per-

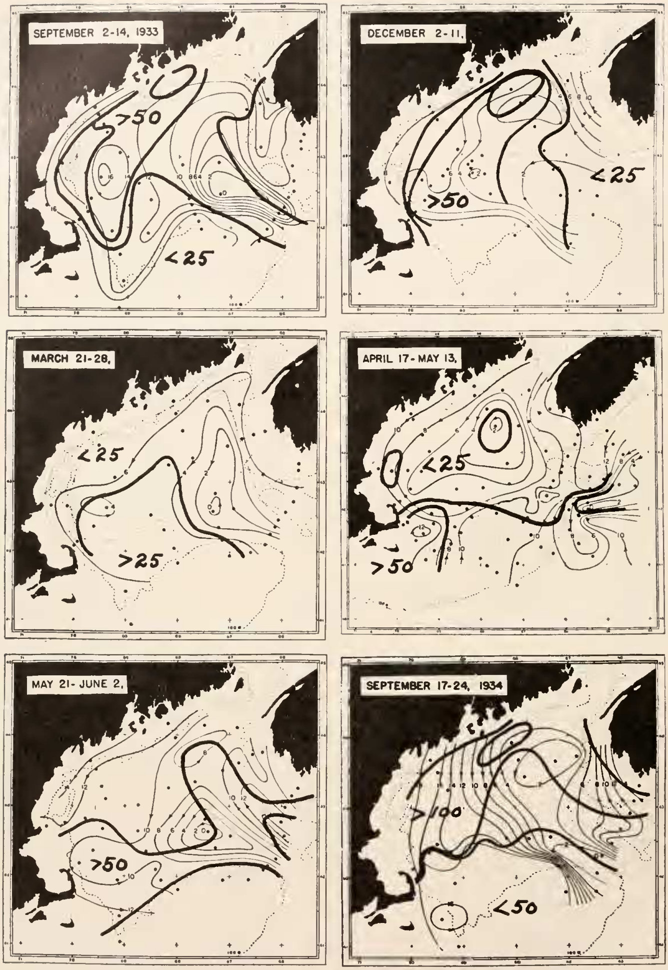

FIG. 6. Dynamic contour charts showing the theoretical circulation of the Gulf of Maine at the surface between September, 1933 and September, 1934. The heavy contours, taken from Figs. 1 and 2, indicate the relative density of population at the time of each cruise.

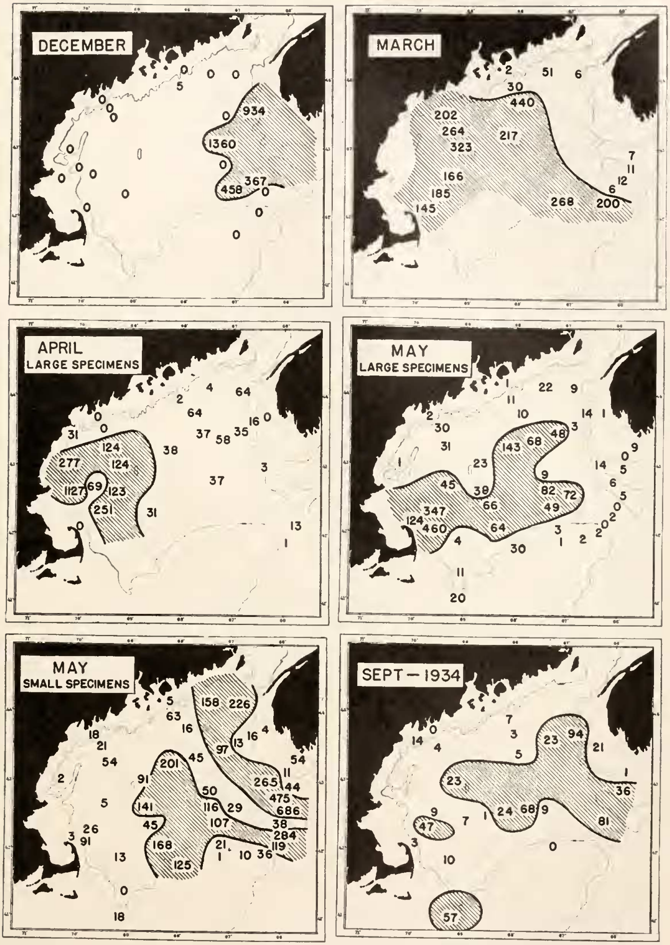

FIG. 7. The distribution of *Limacina retroversa* in the Gulf of Maine between December, 1933 and September, 1934. The numerals indicate the position and the numbers caught per haul. Compare Fig. 6 for corresponding current diagrams and the coincident distribution of the calanoid community.

mitted me to use some of his current diagrams in advance of the publication of his full report. This study has not only confirmed the more general conclusions of Bigelow, but gives the best available evidence of the actual character of the circulation at the time of our collections.

The zoöplankton population is not distributed uniformly in waters of various depth but tends on the whole to congregate in the upper 100 meters (Bigelow, 1926, p. 93). In many species, particularly of the numerically important copepods, there is a pronounced diurnal vertical migration which has been studied in the Gulf of Maine by Clarke (1933, 1934). At a station in the deep part of the Gulf, he found that *Calanus* and *Metridia* migrated to a depth of 120 meters or more during the daytime and moved upward to levels of from 6 to 42 meters at night. On Georges Bank *Calanus* was confined to the surface strata, undergoing very limited migration, but *Metridia* carried out an extensive vertical migration. Consequently the population cannot be identified exclusively with any particular layer and any attempt to correlate its distribution with the drift of the water is complicated by the undoubted migration of the animals to and from layers of different depth moving with different velocities and in some places without doubt in different directions. As a first approximation, however, it is reasonable to assume that considerable volumes of the more superficial water, unconfined in its movements by shoals, will retain for appreciable periods a unity sufficient to permit a definite population to be identified with it. The horizontal movement of the water at a depth of 40 meters should be fairly representative of the layers in which the zoöplankton chiefly occur within the Gulf. At this depth the water is unobstructed in its movements by any considerabe shoals. We have reproduced the dynamic contours at a depth of 40 meters in a recent paper (Redfield and Beale, 1940, Fig. 10). The surface circulation does not differ in important detail from the charts representing conditions at 40 meters. It shows a somewhat closer correlation with certain features of the plankton distribution. Charts showing the gradient currents at the surface have consequently been employed in preparing Fig. 6.

Additional evidence of the character of the circulation, and particularly of its influence in actually transporting a pelagic population, is provided by the distribution of *Limacina retroversa* in the Gulf during the period of this survey (Redfield, 1939). These organisms appeared en masse in the Browns sector in December and their drift was followed as they spread across the Gulf. In four months they had arrived in numbers in the western basin, having spread along the northern margin of the Gulf in the course taken by the receding center of the zoöplankton population (Fig. 7).

The Relation of Population Distribution to the Hydrography of the Gulf

The following theory is proposed to account for the seasonal fluctuation of the population of zoöplankton. The superficial current, or non-tidal drift, consists of a great cyclonic eddy. The eddy is augmented by the inflow of water on the eastern side from over the Nova Scotian Banks. The inflow is compensated for by the escape of water to the south and east across the end of Georges Bank. The relative volumes of inflow and outflow vary from season to season and year to year. In the winter and early spring the inflow is sufficiently great to replace a considerable part of the eddy with water new to the Gulf. This "new" water is relatively barren and does not develop a more considerable population until conditions become favorable for growth and reproduction in the spring, by which time it has extended over the entire northern half of the eddy. Meanwhile an equal part of the older water, which had been in the Gulf during the preceding summer, escapes from the Gulf. The remainder occupies the southern half of the eddy. This water supports a rich population grown up during the previous summer and only moderately diminished by the conditions of the winter. In spring and summer the inflow and outflow diminish and the southern half of the eddy carries an increasing quantity of water northeasterly toward the Bay of Fundy, with the result that this water enters a second circuit of the Gulf, carrying with it a large population which enriches the northern half of the eddy during the late summer and fall. This region may also be enriched by an inflow of water from the Nova Scotia banks which carries a considerable population at some seasons.

The adequacy of this theory is demonstrated in Fig. 6, in which contours representing the areas of relative abundance recorded in Figs. 1 and 2 are transposed upon diagrams of the dynamic gradients in the surface waters. The general distribution of these contours was established without reference to the current diagrams.

In September, 1933, the center of population lay in relatively quiescent water along the northern margin of the Gulf and extended southwestward to occupy a secondary eddy over the western basin. A more scanty population occupied the Cultivator sector. Over the Nova Scotian Banks a condition of slack water existed with no evidence of indraft except along the eastern margin of the Eastern Channel. This water was scantily populated. A marked eddy occupies the Eastern Channel with its offshore component lying on the western side. This includes a tongue of richly populated water in which much plankton is being carried out of the Gulf. During this period the population is being impoverished by this outdraft.

By December a strong indraft of water over the Nova Scotian Banks has commenced carrying into the Gulf water containing a scanty population. This water contains abundant *Limacina* which occupy the eastern area in which catches of less than 25 cc. of plankton occurred. (Figure 7.) Compensatory movements must be expelling richly populated waters over Georges Bank.

By March scantily populated water has extended along the entire northern margin of the Gulf, carrying with it the population of *Limacina*. Considerable volumes of zoöplankton were then taken only in the southwestern quarter where relatively slack water is found. A small eddy occupies the western basin and in it *Limacina* mingle with considerable remnants of the copepod population. In the eastern half of the Gulf the major eddy is well marked. Along its eastern side water still enters the Gulf scantily populated with copepods and now containing very few *Limacina*. Its western arm is carrying many *Limacina* out to sea.

In April the character of the circulation changes abruptly from a loop to a closed eddy. Invasion of water from offshore has come practically to an end and considerable numbers of copepods which occur at the mouth of the eastern channel have no opportunity of entering the Gulf. In the west a small concentration of copepods persists near the South Channel. The *Limacina* population is now centered over the western basin, but considerable numbers appear to have spread eastward along the southern and eastern arcs of the great eddy.

Up to this time the movements of water and of the populations of copepods and *Limacina* appear to be perfectly correlated. There can be no doubt that the inflow of barren water from the east has displaced a large part of the copepod population from the northern and eastern part of the Gulf, forcing it out to sea over the eastern end of Georges Bank.

In May and June the loop-like character of the circulation reëstablishes itself, but a considerable eddy persists in the center of the loop. Reproduction now increases the population everywhere. The copepod population occurs in greatest numbers in the slack water of the western basin. From there a rich band extends along an east-flowing current out to sea over the Eastern Channel. A part of this eastward extension has evidently been caught in the recurrent eddy and carried northward toward Mount Desert. Richly populated water found in the North Channel appears to be moving out of the Gulf. The only water entering the Gulf at this time lies along the east side of the Eastern Channel and appears to be scantily populated. It seems improbable that a considerable population is being recruited at this time. The increasing numbers observed in the eastern region apparently come from the southern and western region.

The distribution of *Limacina* in May–June agrees with this interpretation of the water movements. The population of large specimens, which had wintered in the Gulf, extends eastward along the southern side of the Gulf, and northward along the eastern side of the eddy. The small specimens, new to the Gulf, lie along the inflow and about the center of the eddy. Others follow the eastern arm of the inflow which recurves along the Nova Scotia shore.

By September, 1934 conditions have reëstablished themselves much as they were a year before. The southern half of the Gulf appears to be occupied by the more scanty population, presumably derived from the barren water which lay to the north in the spring. This is trapped in a dead water. A large population has grown up in the eddy which forms each summer in the northeast quarter and well-marked currents exist to carry this population to the southeast. The current flow into the Gulf is stronger than the year before and appears to bear an abundant population from offshore into the eastern side of the Gulf. This is the only indication that the copepod population is enriched by exchanges with offshore waters in the course of the year.

The small numbers of *Limacina* which occupied the Gulf in September, 1934 occurred in greatest numbers along the course of the inflowing water.

It is unfortunate that a more complete survey was not made between June and September. The events which are least clear are those leading to the development of the exceptional populations in the Mount Desert region in late summer. It is not certain that these may not have been recruited from offshore during the summer. The circulation calculated for May–June would appear to transport the richer water then found in the south out to sea more effectively than toward the northeast. Possibly the rich population extending northward toward Mount Desert arrived there before the loop-like eddy reestablished itself. There are, however, several considerations which support the view that the population of the northeastern sectors is recruited from the southern part of the Gulf in early summer.

Fish (1936) records the invasion of the coastal waters of Maine by *Calanus finmarchicus* larvae in June which he assigns to a " western stock." These he believes to be absent from the eastern half of the outer Gulf earlier in the season, and to have drifted in toward the Maine coast from the southwest. The larvae of this stock greatly outnumber those of an " eastern stock " which entered the Gulf from the Scotian Banks in April.

Drift-bottle observations indicate an actual movement of water from the southern toward the northeastern quarter of the Gulf in summer (Bigelow, 1927). There can be no doubt that the surface water does move in this direction, dynamic calculations notwithstanding.

It is possible that lateral mixing along surfaces of equal density may permit rather extensive exchanges of water across gradient currents (Iselin, 1939). In particular, according to a principle developed by Parr (1936), stratification in turbulent waters leads to increased lateral mixing. Thermal stratification in the Gulf of Maine was well developed in May, 1934, and its onset may have facilitated the transfer of well-populated waters across the eddy. It is noteworthy that during May a considerable intermingling of *Limacina* with water rich in copepods occurred along the southern side of the Gulf. It is also noteworthy that the distribution of *Limacina* became much more homogeneous in May than it had been earlier. This was true also of the plankton population as a whole, as Fig. 4 shows. Lateral mixing deserves more study by biologists, as Iselin has pointed out, for it may well be an important factor in preventing local breeding stocks from being swept out of embayments by directional currents.

In summary, the hydrographical evidence appears to support the view that the scanty population of the eastern sectors in midwinter is due to their occupancy by the barren water, which appears in the Browns Bank sector in December and can be traced until it enters the Massachusetts sector by May. The eastern and northern sectors thus receive an influx of relatively barren water in midwinter when the climate is unfavorable for further growth of the population. In the early summer, on the other hand, water drifts from the southern part of the Gulf into the northeastern sectors. This water is about to commence its second circuit of the Gulf and carries with it a population which has already grown to some magnitude in the sectors from Massachusetts to Georges Bank by the end of May.

In contrast to this, the sectors of the western basin receive in winter water which had acquired an abundant population in the Mount Desert and Seguin sectors during the fall. Although there is some destruction of the organisms at this season, it is not sufficient to reduce the numbers greatly. With the coming of spring, this water moves on to be replaced by the barren water found in the northern sectors during the winter. But as this water warms, its population grows and rapidly comes to equal that of the water it replaces. The uniformity of the population in the western basin is due to the fact that a rich fauna arrives there coincident with unfavorable conditions in winter, and a scanty fauna comes to occupy the region during the period most favorable for growth.

The Average Monthly Catch

The monthly catch obtained by averaging the mean values for all sectors during each cruise is given in Fig. 8. The average monthly catch remained constant at about 40 cc. per square meter from June to December, 1933. The values fall markedly from January through April. This is undoubtedly due to the destruction of the population by winter cold. At this period, however, large quantities of water poor in population are entering the Gulf and an equivalent quantity bearing a richer population is leaving, thus accounting for much of the loss.

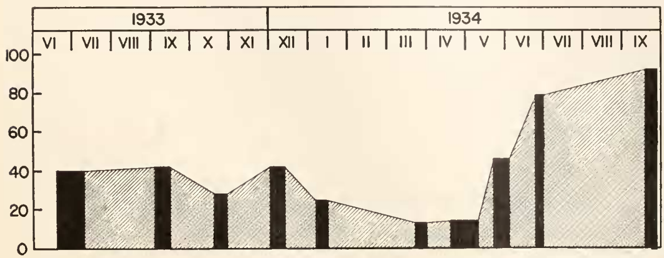

Fig. 8. Average catch for entire Gulf during the period of survey. Ordinate: cubic centimeters of zoöplankton per square meter of sea surface. The black bars indicate the actual period occupied by each cruise.

In May the average population begins to increase suddenly and its growth continues at a diminishing rate until the last observations in September, 1934. The population as a whole is then twice as great as that encountered during the preceding year,—the average haul being 90 cc. per square meter.[2]

[2] Bigelow found that the zoöplankton was at its lowest ebb in late February and the first half of March in 1920. At this time his catches varied from 75 to 25 cc. per square meter measured wet (equivalent to 15 to 5 cc. measured "dry"). Our catches in March averaged 13 cc. and for April 8 cc. per square meter measured "dry." The 1934 year appeared to be a late year and was initiated by an unusually cold winter. The April observations are perhaps misleading since collections were not made in the parts of the Georges and Cultivator sectors where the highest population was expected. Bigelow considered 100 cc. wet (20 cc. or more measured dry) to be representative of the Gulf in midsummer, a value much smaller than our average of 40 cc. in 1933 and 80 cc. in 1934. His largest catch of 425 cc. (85 cc. "dry"), made in September, 1915, does not exceed the average value obtained in September, 1934 for all sectors. It must be remembered that he employed a different method of measuring his catch and nets which doubtless differed from ours in efficiency.

The Total Annual Production and Exchange

The average catch throughout the period of the survey in each sector,—obtained by averaging the mean figures obtained at the time of each cruise—is given in Fig. 9.[3] It is noteworthy that the catch increases progressively as one passes along the course of the water movement from its inflow over the Browns Bank sector to its exit across the end of Georges Bank. The longer the water has been in the Gulf, the greater its population.

The average catch is greatest in the Mount Desert sector and is an exception to the foregoing tendency. We suggest that this is due to the movement of water, which has already completed the circuit of the Gulf and is rich in plankton, from the southern sectors into the Mount Desert sector during the summer. The Mount Desert sector thus virtually occupies a position at the end of the series during the months when its population is greatest.

The average haul for all sectors of the Gulf and at all cruises is about 40 cc. per square meter of "dry" plankton. If the area of the Gulf be taken at 36,000 square miles, this would indicate a total population of about 3.7×10^{12} cc. or some four million tons.[4]

The standing crop does not give a measure of the rate of production of the population, since it reflects merely a balance between rate of growth and death and the gains and losses in the population by movement into or out of the region. It is clear from Fig. 8 that the crop increased by nearly 80 cc. per square meter of surface between May and September. This represents a net gain of some eight million tons.

The observations make it apparent that the Gulf loses at least one half of its population through the escape of water over Georges Bank and the Eastern Channel each winter. There is no evidence that water enters the Gulf at any time carrying a richer population than that obtaining there at the time, and only in September, 1934 was water found to enter the Gulf in which the copepod population was not distinctly

[3] This method of averaging avoids overweighting the yield of these sectors in which an unusual number of rich hauls were made at a time when the population was particularly large, as would be the case if all catches were simply averaged.

[4] In discussing the productivity of the Gulf of Maine, Bigelow concluded that the population was greatest over a band extending from the Massachusetts coast to Penobscot Bay and the Bay of Fundy. The areas occupied approximately by our Seguin sector and the greater part of the Cultivator and Georges Bank sectors were considered barren. His conclusion that the southern sectors are barren certainly rests on insufficient evidence, since only two hauls are recorded. Our richest haul was obtained over the southeastern deep in June, 1934 and the Cultivator and Georges sectors are the most populous sectors excepting Mount Desert throughout the year as indicated. Our observations agree that the Seguin sector is relatively unproductive. Its best season was the fall of the year, a time when Bigelow made relatively few cruises. Several of our richest hauls were made off Seguin in September, 1934.

scanty. Unless further observations during the summer should prove the contrary, it may be concluded that the Gulf is a region of production for the calanoid community which supplies immigrants to the southern banks in quantity, but receives relatively unimportant recruitments from the regions to the eastward.

The Growth of the Population in the Moving Mass of Water

If the interpretation which we put on the data is correct, it is certain that observations made at a geographically fixed point, or standard station, tell little about the fluctuations of any unit of the population. We record simply a series of events distributed in space as they drift past in the course of time. The conditions we observe today are not determined by the events we observed yesterday. The curves of population growth presented in Fig. 5 are grossly misleading if they are interpreted to represent the history of any biologically continuous unit.

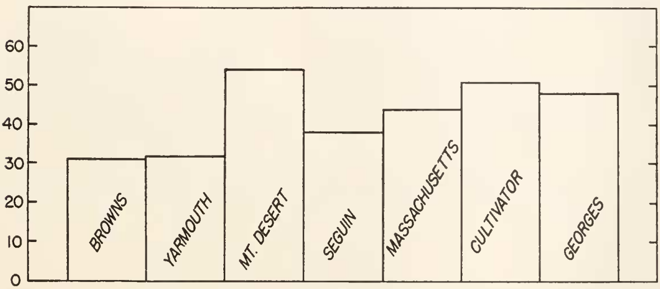

Fig. 9. The average catch in each sector during the period June, 1933 to September, 1934. Ordinate: cubic centimeters of zoöplankton per square meter sea surface.

By taking account of the rate of drift of the water, it is possible to select appropriate stations to show the growth of population in a unit volume of water as it is carried about the Gulf of Maine eddy at the apparent rate of its non-tidal drift. While the result is both an abstraction and an approximation, it probably indicates the true history of events better than the usual curves of population fluctuation. Figure 10 represents the apparent growth of the population of a unit mass of water entering the Gulf in December and recognized by the presence of *Limacina*. As the season advances it is carried across the northern sectors, arriving by May in the offing of Cape Ann. During this period the population decreases by about one-third, but in May as it crosses the western basin rapid growth occurs with the result that in midsummer it has reached the value of 50 cc. per square meter, greater than the yearly average for the Gulf as a whole. The unit may now drift out of the Gulf across the end of Georges Bank in late summer or it may drift northeasterly into the Yarmouth sector to commence a second circuit of the Gulf. Its numbers grow meanwhile to over 100 cc. per square meter. After January 1, high mortality again reduces the numbers to about one-third or to 30 cc. per square meter, as it crosses the Massachusetts sector in March. In May growth recommences and by

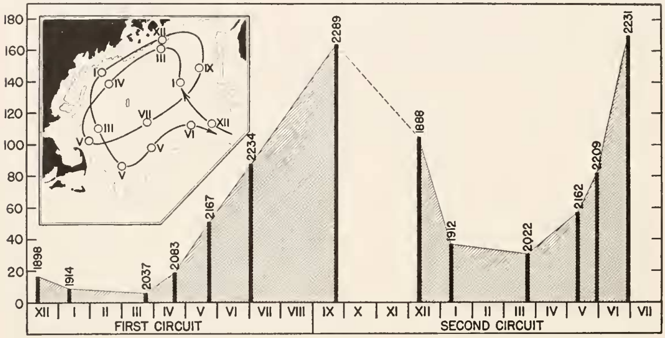

Fig. 10. The growth of population in a mass of water assumed to move along course indicated in inset. Ordinate: volume of zoöplankton in cubic centimeters per square meter sea surface; abscissa, time in months. The black bars indicate the volumes caught at the selected stations. The positions of these stations and the month of collection are indicated on the inserted chart.

midsummer it reaches the Georges sector, having attained the record volume of 170 cc. per square meter. Its history may be terminated by supposing it to be carried out of the Gulf at this time.

Figure 10 is presented because it illustrates the possibility of taking account of the current system in an ecological analysis. It may be pointed out that the life history of any individual species might be treated in a similar way.

Annual Fluctuations in Population

The average catch at all stations was more than twice as great during the summer of 1934 as during the same period in 1933. Since the hauls were numerous, widely spaced, and all made with the same technique, there can be little doubt of the significance of this observation. The difference is the more striking in that an unusually severe winter preceded the richer year.

The suggested theory offers a tentative explanation of such fluctuations. The poverty of the water in the northern half of the Gulf in winter seems due to the introduction of a large volume of relatively barren water from the Scotian Banks. It is suggested that more of this water enters in some years than in others, and that the population of the Gulf is impoverished in proportion to the magnitude of this inflow. The longer water remains in the Gulf, before being replaced by new water, the richer its population becomes.

A number of facts support this suggestion. It is well known that the magnitude of the inflow varies from year to year. The inflow during the winter of 1934 seems to have been of shorter duration than usual, having been completely terminated by a strong movement of water from the Gulf over the North Channel and adjoining banks in May. The movement was apparently underway in the latter part of April, as the current diagrams show (Fig. 6). Drift bottles set out by Dr. Herrington off Cape Sable at that time were recovered to the eastward. In contrast to this, Bigelow observed the invasion of the Gulf by Nova Scotian water to continue until May or June and to result in a cooling of the eastern part of the Gulf long after the other parts had commenced to warm. He speaks of the invasion as a phenomenon of spring, whereas in 1934 it terminated before the end of winter.

It is also possible that differences in the circulation such as those observed in September, 1933 and 1934 may cause the population of the Gulf to be augmented from external sources to a different degree each season.

Since the water flowing into the Gulf over the Nova Scotian Banks is less saline than that occurring at like depth within the basins, a small influx of this water should be followed by a summer of relatively high salinity. The superficial water of the Gulf was exceptionally salt in 1934. It appears to have been as salt or salter than in 1915, the most saline year recorded by Bigelow. In 1933, on the other hand, the water was quite as fresh as in 1914 and 1916, the least saline of those he recorded. A correlation between salinity, productivity, and annual inflow over the Scotian Banks is strongly suggested. Systematic annual observations would serve to test this relation, and should it prove general, might lead to an understanding of the yearly fluctuations in commercial fisheries.

The Distribution of Petrels and Mackerel

The zoöplankton supplies food for various predators. Their distribution may be expected to be influenced secondarily by the hydrographic factors which determine the abundance of the calanoid community.

Petrels

These birds appear to feed upon zoöplankton or their products. They pick up whatever scraps of organic matter they can find, gathering about fishing vessels, following ships, and feeding about the carcasses of dead whales and seals. There is a general belief that they pick up droplets of oil from the surface of the water, and their stomachs frequently contain an oily fluid which they eject when captured. It seems

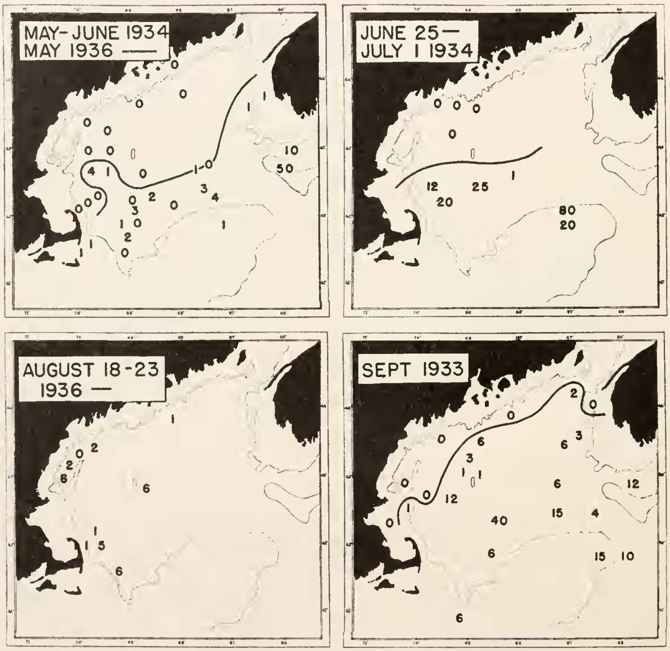

FIG. 11. Numbers of petrels observed in different parts of the Gulf of Maine during cruises at various times of year.

more probable that this is derived directly from their food. Wilson (1907) states that the food of the Wilson's petrel, which he observed in the antarctic, consists of minute crustaceans. The natural food of the Leach's petrel, according to Bent (1922, p. 143) " includes shrimps and other small crustaceans, floating mollusks, perhaps small fishes occasionally, and probably many other forms of minute marine animals which are found swimming on the surface or in floating masses of seaweed."

Wilson's petrel is the common petrel of the Gulf of Maine. Leach's petrel, though a breeder along the coast of Maine, is much scarcer. Not more than one petrel in twenty or thirty observed at sea is of this species. Wilson's petrel breeds in the south Atlantic during December, January and February and does not reach the Gulf of Maine until May. None were observed during the cruise of April 19–23, 1934. In cruises in May, 1934 and 1936 petrels were observed in small numbers in the southern and eastern regions, where at that season the largest zoöplankton hauls were taken, but were absent from the northern sectors which at the time were occupied by relatively barren water (Fig. 11). During

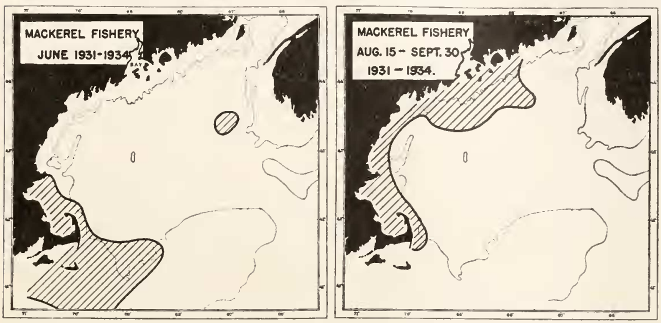

Fig. 12. The areas occupied by the mackerel fishery during the early and late summer 1931–1934.

a cruise from June 25 to July 1, 1934, petrels were present in larger numbers in the southwestern quarter, but were not observed in the Seguin sector. On August 18 to 23, 1936, however, petrels were observed regularly at stations made in the northern side of the Gulf. In September, 1933 petrels were observed everywhere in the Gulf except at a few coastwise stations along the shore. At this time all sectors supported an abundant population of zoöplankton.

It appears that when Wilson's petrel first arrives in early summer it remains confined to those sectors of the Gulf which then support the richest plankton.

Mackerel

In the Gulf of Maine these fish have long been known to feed on calanoid copepods and are known to eat various other crustaceans which compose the bulk of the zoöplankton (Bigelow, 1926, p. 102). It is not surprising in consequence to find a correlation between the seasonal distribution of this fishery and of the local abundance of zoöplankton.

Dr. Settee has kindly placed at my disposal the very complete records made by the U. S. Bureau of Fisheries showing the places in which mackerel have been taken during recent years. The mackerel fishery begins in New England waters with the arrival of the fish south of Cape Cod in May and June. The fish are first taken along the shores of the Gulf of Maine in June, chiefly within the 100-meter contour from Cape Ann to Cultivator shoal. At this time heavy catches are also made along the east coast of Nova Scotia and northward to Gaspé (Settee and Needler, 1934). The July fishery has much the same distribution, though tending to spread farther east along Georges Bank and also in some years along the western part of the coast of Maine. In August and September a considerable fishery is conducted in the northern side of the Gulf, from Mount Desert westward, and southward as far as Cape Cod (Fig. 12). During these months the fishery in the Bay of Fundy is at its height, 37 per cent of the total catch being made during each of these two months, whereas less than 10 per cent is taken in any one of the preceding or following months.

In interpreting these facts the peculiarities of the fishermen as well as of the fish must be borne in mind. Mackerel are now marketed fresh and are landed chiefly in Boston. The fishermen consequently do not fare farther from this port than is necessary. The takings of mackerel do not reflect accurately the total distribution of the fish, but only their availability to the Boston market. It seems sufficiently clear that in early summer mackerel are available chiefly along the southern shores of the Gulf; that by late summer their abundance has shifted to the northern shores, including the Bay of Fundy. This is the distribution of the maximum of zoöplankton population as well. Whether the mackerel follow the plankton as it drifts around the great eddy, or cut across to meet its advance from the east in the late summer, as the fishermen undoubtedly do, cannot be told.

Thus there appears to be a general correlation between the distribution of the zoöplankton, the occurrence of petrels, and the capture of mackerel.

Summary

1. The seasonal and geographical fluctuations of the abundance of the calanoid community of the Gulf of Maine are described.

2. The shift in the center of abundance is closely correlated with the superficial circulation, deduced from hydrographic observations and the drift of an invading population of *Limacina*.

3. The principal factor influencing the distribution of population density is the inflow of relatively barren water from the Nova Scotian coast in winter.

4. The Gulf appears to be an area from which the calanoid community spreads to other waters, but which receives relatively small recruitments from without its borders.

5. A breeding stock is maintained by the establishment of a recurrent eddy in the late spring.

6. Estimates of annual productivity and seasonal mortality are given.

7. The distribution of petrels and of the mackerel fishery appears to be correlated with the distribution of zoöplankton.

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